SYSTEMATIC POSITION OF MOLOSSIDAE – AN EMBRYOLOGICAL ANALYSIS[1]

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(With two text-figures)

At present, morphological and anatomical characters constitute the main criteria for classification of eutherian mammals, since other criteria are not available for most mammalian groups. But these systems of classification based on morphological characters, do not necessarily reflect the phylogenetic affinities of various subgroups among mammals. This has been convincingly argued by Mossman (1937, 1953) in his analysis of foetal membrane characters of various grades of eutherian groups. In the absence of adequate data from palaeontology, cytology, genetics, serology and such other disciplines, evidence from embryology assumes considerable significance for determining taxonomic position and phylogenetic affinities among lower grades of taxa, such as Super-families and Families.

So far all taxonomists have placed Pteropodidae at the beginning and Molossidae along with Vespertilionidae within the Super-family Vespertilionidae, at the other end in the taxonomic hierarchy of the Order Chiroptera (Simpson 1945, Ellerman and Morrison-Scott 1951, Honacki *et. al.* 1982, Koopman 1984, Hill and Smith 1985). Jones (1917) examined the anatomy of the female genitalia of many species of bats and suggested that Chiroptera is a polyphyletic group, in which are included members derived from divergent ancestors.

Mossman (1937), basing his conclusions on foetal membrane characters, suggested that Megachiroptera share characters with Rodentia, whereas Microchiroptera are closer to Insectivora. It must, however, be conceded that very little information was available about the embryology of most families of Microchiroptera at that time. Moghe (1951), in his study of the embryology of *Pteropus giganteus giganteus*, mentioned, "the two groups (Megachiroptera and Microchiroptera) are widely separated from each other in a large number of other characters and probably represent independent offshoots from some primitive insectivore". (Parentheses ours.) On the basis of embryological characters of four microchiropteran families, Gopalakrishna (1958) mentioned, "the Megachiroptera and Microchiroptera are not as divergent as formerly believed. Many similarities and transitional characters are now apparent between the two sub-orders".

Luckett (1979), making an analysis of anatomical and embryological characters, suggested that the group Chiroptera is monophyletic, but he placed Molossidae as far removed from Pteropodidae. Gopalakrishna and co-workers (1981, 1983, 1987, 1988, 1989) examined the anatomy of the female genitalia, blastocyst-uterus relationship and development of foetal membranes of several families of bats, and postulated that not only is Chiroptera a monophyletic group but that the taxonomic hierarchy currently maintained by systematists needs some changes. One such suggestion was that the systematic position of Molossidae needs to be re-examined.

The basic premise for the present report is that in eutherian mammals embryological characters are far more conservative than are morphological characters, since development takes place in a constant environment within the uterus, while morphological characters are directly influenced by the environment and are therefore adaptive. Hence, similarities in embryological characters, according to Mossman (1937, 1953), indicate a closer phylogenetic affinity than similarities in morphological characters.

The present report is based on recent publications and ongoing work in this laboratory on the embryology of four molossid species, namely *Chaerephon plicata* (Gopalakrishna *et al.* 1989),

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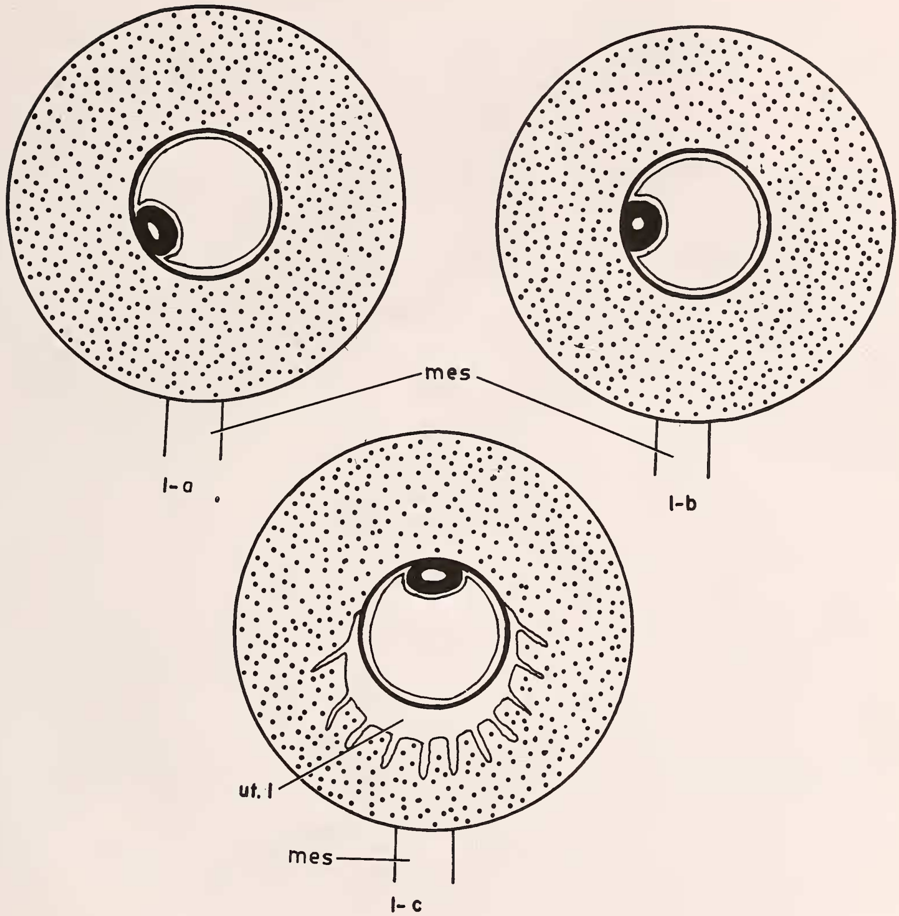

Fig. 1. a-c. Uterus-blastocyst relationship at the time of implantation in (a) Pteropodidae, (b) Molossidae and (c) Vespertilionidae. The dark circle with a white central area represents the embryonic mass containing the primitive amniotic cavity. mes : mesometrium; ut. l : uterine lumen.

Tadarida aegyptiaca (Sandhu 1986), *Tadarida trageta* and *Molossus major aztecus* (*M. molossus*) (Gopalakrishna and Badwaik in press) and comparing the results with what is known of the embryology of other relevant families, namely Pteropodidae and Vespertilionidae.

Such a comparison reveals that the molossids share more embryological characters with pteropodids than with vespertilionids. Among pteropodids, implantation of the blastocyst is partly interstitial with the embryonic mass oriented towards the lateral side in *Pteropus giganteus* (Moghe 1951). In *Rousettus leschenaulti* (Karim 1976) and *Cynopterus sphinx* (pers. obs.) blastocyst implantation is superficial and the embryonic mass is oriented towards the tubo-uterine junction, which is sub-terminal and towards the lateral side of the uterus. The orientation of the embryonic mass in the implanting blastocyst is lateral in all the molossid bats (Sansom 1932, Pendharkar and Gopalakrishna 1983, Sandhu 1986).

Secondly, in Pteropodids and all molossids the blastocyst establishes contact with the uterine

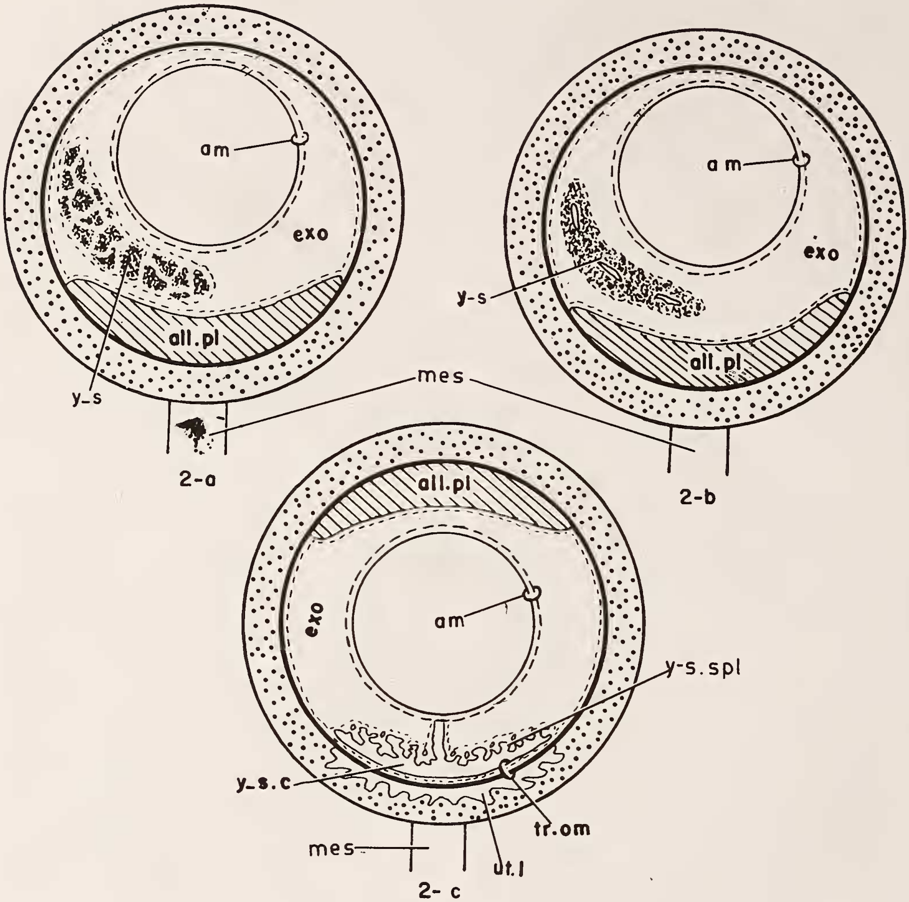

Fig. 2a-c. Definitive arrangement of foetal membranes in (a) Pteropodidae, (b) Molossidae and (c) Vespertilionidae all. pl : allantoic placenta; am: amnion; exo: exocoelom; tr. om: trilaminar omphalopleure; y-s: yolk sac; y-s.c.: yolk sac cavity; y-s. spl: yolk sac splanchnopleure. Other legends as in Fig. 1.

wall on all sides, resulting in the obliteration of the uterine lumen at the level of implantation. This situation differs from what obtains in all vespertilionids, in which the blastocyst attaches itself to the antimesometrial side of the uterus by its embryonic pole, and the abembryonic region of the wall of the blastocyst lies freely hanging into the uterine lumen on the mesometrial side of the uterus (Fig. la-c).

In both Pteropodidae and Molossidae an extensive yolk sac placenta is formed on all sides of the uterus except where the embryonic plate intervenes between the yolk sac and the uterine wall. This is at first non-vascular, but soon becomes vascularised and forms the chorio-vitelline placenta during early stages of pregnancy. In Vespertilionidae, on the other hand, only the lateral wall of the yolk sac forms the yolk sac placenta, while the abembryonic region remains non-vascular and free.

The unique modification of the yolk sac into a solid gland-like structure in both Pteropodidae (van der Sprenkel 1932, Moghe 1951, 1956; Wimsatt 1954, Gopalakrishna and Karim 1974, Karim *et. al.* 1979, Gopalakrishna and Karim 1981) and Molossidae (Stephens 1962, Stephens and Easterbrook 1968, 1969, 1971; Sandhu 1986, Gopalakrishna *et al.* 1989) is unmatched in any other family of Chiroptera – and in fact in any other mammal. The yolk sac splanchnopleure becomes free and undergoes progressive collapse until the yolk sac lumen is completely obliterated in Pteropodidae. In Molossidae the yolk sac lumen is reduced to a few isolated, very narrow streak-like spaces here and there within the solid yolk sac.

In both families the endodermal cells undergo enormous hypertrophy and form acinus-like groups; the mesodermal cells form the loose matrix and the outer covering to the gland-like yolk sac. In Vespertilionidae (Ramaswami 1933, Wimsatt 1945, Enders and Wimsatt 1968, Gopalakrishna 1950, Gopalakrishna and Sapkal 1974 Ramakrishna and Madhavan 1977, Gopalakrishna *et al.* in press) the yolk sac lumen persists as a continuous space between the proximal invaginated, folded vascular splanchnopleure and the distal free trilaminar omphalopleure (Fig. 2a-c). The uterine lumen persists on the mesometrial aspect of the uterus throughout gestation.

The definitive allantoic placental disc is mesometrial in both Pteropodidae and Molossidae, whereas it is squarely antimesometrial in Vespertilionidae (Fig. 2a-c). With respect to the histological structure, the placenta is endotheliochorial in *Pteropus* and *Cynopterus* and haemochorial in *Rousettus*. In molossids a diffuse endotheliochorial chorio-allantoic placenta occurs concurrently with a small mesometrially located discoid placenta until about the third quarter of gestation. The discoid placenta is haemochorial. However, during the final quarter of gestation the diffuse endotheliochorial allantoic placenta disappears, and only the mesometrially located discoid haemochorial placenta persists. Molossid bats, therefore, develop both endotheliochorial and haemochorial allantoic placentae. In all vespertilionids the placenta is haemochorial.

It is thus evident that embryological similarities between Molossidae and Pteropodidae and differences between Molossidae and Vespertilionidae suggest a closer relationship between Pteropodidae and Molossidae than between Molossidae and Vespertilionidae. It is, therefore, suggested on purely embryological grounds that Molossidae be separated from the Super-family Vespertilionidae and be placed somewhere between Pteropodidae and Emballonuridae.

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